A Field Study on the Clustering and Movement Behavior of the Limpet *Acmaea digitalis*

BY

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(1 Plate; 3 Text figures)

INTRODUCTION

Acmaea digitalis Eschscholtz, 1833, is one of the more commonly found limpets inhabiting the uppermost rock beaches. Stenotopically it occupies a restricted area in the intertidal zone, an ecological niche that excludes most other members of the genus *Acmaea*.

Its distribution extends from the Aleutian Islands to Lower California; however, it is reported to be in greatest abundance northward of Monterey Bay. Along the coast of central and northern California and probably elsewhere, *Acmaea scabra* and *A. digitalis* occupy the same habitats, often competing for shelter and possibly for food (Test, 1945). Although they are competitors, generally their rock preferences and dispersion are somewhat different. *Acmaea digitalis* frequently restricts itself to a narrow band along the upper vertical rock surfaces. Its cohabitant, more solitary in nature, prefers both the vertical and horizontal rocks with a slightly broader seaward range (Sutherland, 1970). However, at the lower limits of its vertical range, *A. digitalis* has been observed sharing horizontal slopes with *A. scabra,* especially where there is a high density of barnacles and algal growth (Haven, 1971).

Along the vertical rock surfaces, where the substrate permits, *Acmaea digitalis* will often be found resting in clusters with members of the same species. This clustering phenomenon, if occurring, has not been described in other west coast members of this genus.

It is generally recognized that limpet movement is initiated by the splash of the incoming tides. As the water level rises, their activity and range of movement increase. During an ebbing tide, the reverse pattern occurs, for as the water action subsides, the limpets regroup and appear to rest until the tidal cycle recurs. Their movements are apparently directed towards foraging and grazing on the microscopic algal film that grows on the rocks (Test, 1945). However, some movements can be attributed to seeking protection from direct exposure as they find shelter in cracks and crevices to avoid prolonged periods of direct sunlight.

In addition to this study, a few others have been undertaken to investigate the movement and clustering behavior of this particular species. Millard (1968) conducted a study at Pacific Grove, California, on the clustering behavior of *Acmaea digitalis* on granite rocks. Clusters of the animals were observed to shift their position from day to day, and they did not occupy exactly the same location or same amount of space from one day to the next. Although the clusters remained intact, there was a constant daily replacement occurring with new members taking the place of limpets leaving the cluster population. Millard's study indicated that limpet clustering was somewhat different from aggregations, for limpets regrouped each day in correlation with the tidal rhythms. The investigator offered land isopods for examples of aggregate behavior. After a period of activity, these animals rested in the dampest and shadiest locations available in close proximity with other members.

Miller (1968), also working at Pacific Grove, observed that during stationary periods at low tide, *Acmaea digitalis* orients itself downward and to the right more than any other position. He related his findings to evidence presented by Abbott's (1956) research on the water circulation in the owl limpet, *Lottia gigantea* (Gray, 1834). According to his study, factors resulting from physiological conditions might influence the limpets to assume this downward and to the right posture. However, the advantages of this position have not been clearly demonstrated with *A. digitalis.*

Miller also found that when these limpets are wetted by the incoming tides, they begin to move up on the rock surfaces as the water rises, and downward at periods of lower high tide. When the surf was rough, the entire population was observed to move upward to a higher level and down when the water action subsided. HAVEN (1971) also noted that the vertical movements of *Acmaea digitalis* along the central California coast were correlated with the seasonal changes. These limpets moved downward in the summer months and upward in the winter months.

Studies on homing of the species under investigation were done by MILLER (1968), GALBRAITH (1965), as well as VILLEE & GROODY (1940). FRANK (1964) conducted studies on this phenomenon along the Oregon coast and from his statistical data concluded that, although *Acmaea digitalis* does not exactly home, it does appear to have a home range. In a more recent study of this species, BREEN (1971) suggests that two distinct behavioral types of limpets may exist, those with homing tendencies and those showing non-homing tendencies.

This field study is directed towards 3 major objectives. First, it is to determine if *Acmaea digitalis* of a specific vertical rock microhabitat consistently return and rest with the same members of this microhabitat, or if their clustering behavior in terms of membership is a random occurrence. A microhabitat is defined as a natural protective site in the rocks (fissures, crevices, and depressions, etc.), where limpets cluster and rest together for shelter.

Secondly, it attempts to investigate whether these limpets assume a predominant orientation position during their resting periods. In relationship to orientation, it also attempts to determine whether any observable characteristics, such as contact with other members, might influence their grouping behavior.

Finally, within the scope of this study, it poses the question: are there any observable periodicities occurring in regard to the resting and movement patterns which are displayed by this particular species of *Acmaea?*

METHODS AND RESULTS

This project was initiated in the summer of 1970, and a year later a more comprehensive study was conducted in August, 1971. It was from the latter investigation that the majority of the data for this report was compiled. The observations described below were made at Davenport Landing, Santa Cruz County, California.

The work was carried out on the lower reaches of a vertical sandstone bench in an unprotected area along the open coast (Figure *1*). The specific habitat site consisted of a rock face parallel to the surf which received the full impact of the waves during periods of high tide. This particular rock surface measured 3.9 m $\times$ 2.4 m, and had 2 distinct topographical areas. The upper region was highly weathered and fractured, resulting in numerous small protective spaces where individuals or small groups of limpets could find protection. The lower portion of the cliff contained large smooth expanses with long angular fractures and folds which were adequate to hold larger clusters of limpets.

Below the area of study at the base of the cliff was a zone of abrasion which was surrounded by a composition of coarse sand and wave-washed rock debris. Limpets of this particular study were found restricted to the high tide range between approximately + 5.0 and + 8.0 feet (1.5 m and 2.4 m), but were exposed during tides below the + 4.0 feet (1.2 m) level.

Food reserves in the habitat area consisted of an unidentified microscopic algal film which was found covering a large portion of the rock face in close proximity to the cluster sites. Other macroscopic algal growths which were probably not used for food purposes were also observed in the study habitat. These included large patches of *Ulva* which covered the lower portion of the rock face with dispersed tufts of *Cladophora, Pelvetiopsis,* and *Ralfsia* randomly growing throughout the study site. No clusters or individuals of *Acmaea digitalis* were found resting in the macroscopic algal growth.

Three natural microhabitats were selected, all approximately 1.5 m above the sand base. Each contained clusters of limpets of various sizes and ages. Some immature *Acmaea digitalis* were present in the microhabitats, but those under 5 mm in length were not included as their size made it possible for them to reach areas difficult to observe.

Two of the microhabitats were fissures approximately 25 cm long, one vertical and one horizontal. The third was an irregular and angular depression formed by erosional processes on the cliff face. Thirty *Acmaea digitalis,* 10

Plate Explanation

Figure *1*: Photograph of wave-cut benches looking south from study site. Bases of the cliff provide a habitat for *Acmaea digitalis*
Figure *2*: Photograph of red microhabitat during study. Limpets in foreground and upper right hand corner are tethered to verify movement during the high tide periods

Figure *1*

Figure *2*

from each microhabitat, were marked *in situ* for the tracking part of the study. The identification procedure consisted of marking small colored tags (white, red, and yellow) with consecutive numbers, using India ink. These were attached to the shells with a quick-drying waterproof adhesive. On previous tests this adhesive, Aron Alpha no. 202, proved to be a non-toxic substance and also was found to be superior to the painted coding system used in the initial study.

In addition to the tagged limpets, 2 dummy clusters were positioned on the rock face with the above mentioned adhesive. A dummy cluster consisted of limpet shells filled with plaster of paris and mechanically adhered to the rocks to simulate a natural living cluster. Ten shells were boiled to remove all chemical traces, and another 10 were positioned on the rocks without any pre-conditioning. Both dummy clusters were placed in close proximity to the 3 selected microhabitats, but in unoccupied spaces. It is interesting to note that both of these pseudocluster sites were previously occupied by living clusters used in the previous summer's study.

After marking, and noting their original positions, the limpets were observed each day at low tide, for 10 consecutive days. Two additional periods were also used to observe movement and clustering behavior at high tide. The 10 tagged members of each microhabitat were traced to their resting positions each day with distance and direction in degrees measured. The position and orientation of each marked limpet was noted along with orientation of all other limpets in each of the 3 microhabitats.

On the third day of observation, a number of the marked limpets within the clusters appeared to be prolonging their resting period, and it was suspected that they were not moving during either of the 2 high tide periods. These limpets were then tethered to the rock so that on later observations a shift or change of position would be evident (Figure 2). Metal pegs were driven into the rocks approximately 2½ to 5 cm from each limpet suspected of remaining stationary. A 4-pound monofilament line was tied to the peg and weakly taped to the animal's shell. The tether had enough strength to withstand the force of the waves, but could easily be parted by the limpets on their shifting position or moving away from the cluster site.

In order to determine the stability of the 3 clusters in terms of continued membership, it was necessary to locate the resting site of each marked *Acmaea digitalis* on a daily basis. The observations revealed that 3 activities were occurring within each of the microhabitats. First, there was a periodic turnover of limpets with some moving out of the cluster while others would return to recluster during the period of low water. A residual number of limpets extended their resting period from one observation to the next (see Figure 3), and apparently did not respond to the stimuli of the incoming tide. The third factor observed was that some of the cluster members rotated or reoriented themselves in each of their respective sites. It is believed by this observer that by repositioning them-

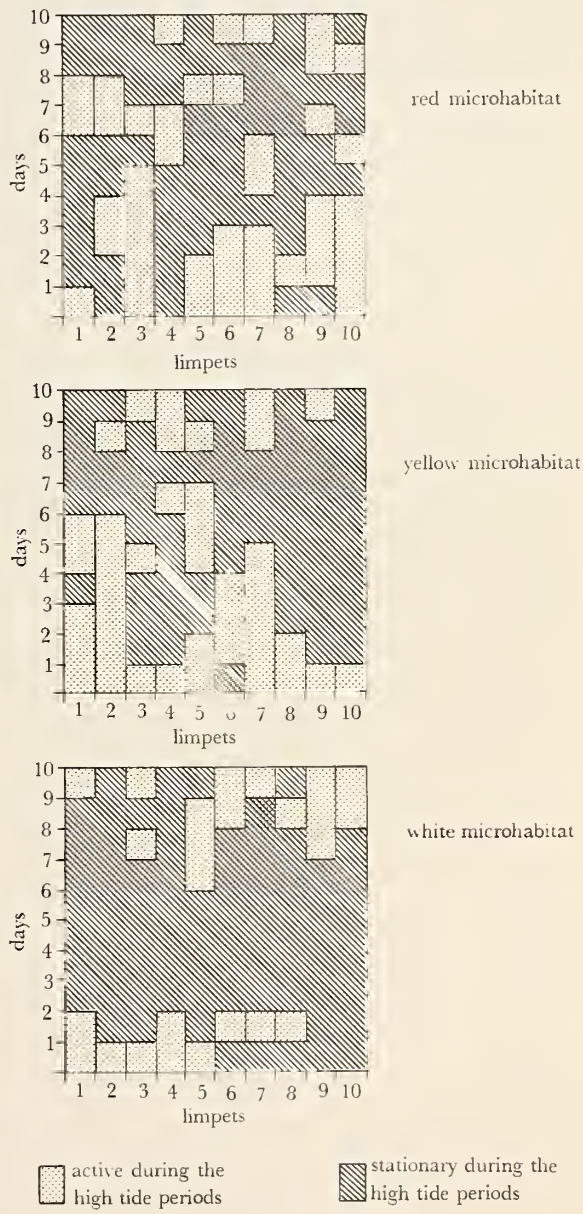

Figure 3

A 10-day observation of the movement and resting behavior of 30 marked individuals of *Acmaea digitalis* illustrated in consecutive days within 3 studied microhabitats selves, they would either benefit from improved locations, or they moved to make contact with other individuals or groups of limpets. The question of contact will be considered later.

Villee & Groody (1940) reported that *Acmaea digitalis* as a group demonstrated high rates of replacement. They interpreted this phenomenon as when one animal moved out, another moved in to take its place. Although a number of specific cases could be cited of this phenomenon, one prime example took place on the 9th and 10th days of the study. Two limpets, marked number 9 and number 10 from the white microhabitat had been resting in relatively the same cluster orientation and position for 8 consecutive days. Number 10 rested in a solitary position on the edge of the cluster 10 cm above number 9, which was in contact with 3 other *A. digitalis*. Each limpet was tethered to verify movement or rotational change. On August 13, number 9 moved up and into exactly the same position of number 10's resting site. Number 10 moved into the center of the cluster and made contact with one other limpet. The following day number 10 returned to exactly the same location and orientation as of August 13. Limpet number 9 returned approximately to the position held initially and made contact with 2 other members of the cluster. It appears that limpet number 10 had left its scar after an extended resting period, and upon returning had found its scar occupied by another member of the cluster.

The permanency of cluster membership was the next behavioral characteristic to be considered. Figure 4 focuses attention on the residual makeup of the clusters. Approximately 20% of the marked limpets from a specific microhabitat returned to their original cluster site where first observed. The figure correlates favorably with my findings of the initial study at the same location in August, 1970. During that investigation 47 limpets were marked, 15 of which were for the individual tracking. Of that number, 25% of the marked limpets returned to the original microhabitat.

The cluster membership remained remarkably stable during the course of the investigation. Even though there was a consistent turnover with new members, and regrouping of some old members on a daily basis, the number in each cluster remained essentially about the same.

Table 1 primarily reflects contact data, but also illustrates a stability in membership from one day to the next. This phenomenon is of interest, for I never found all the available space within each of the 3 sites fully occupied on any one resting period.

The second question of this study concerns the orientation taken by these gastropods as they seek shelter among the folds and crevices of the intertidal rocks. Table 2 accounts for the observations of 411 individual limpet orientations during an 11-day period. Only the clusters within designated microhabitats were used. As previously indicated, *Acmaea digitalis* prefer vertical rock surfaces, but will position themselves on the horizontal plane if so situated on the vertical surface. No one quadrant of the compass suggests a preferred position; however, in analyzing the data there was a slight tendency of the animals to orient with their anterior ends downward as opposed to the anterior ends pointing upward. Rock topography and point of contact with other limpets seemed to account for many of the positions taken. For example, Table 2

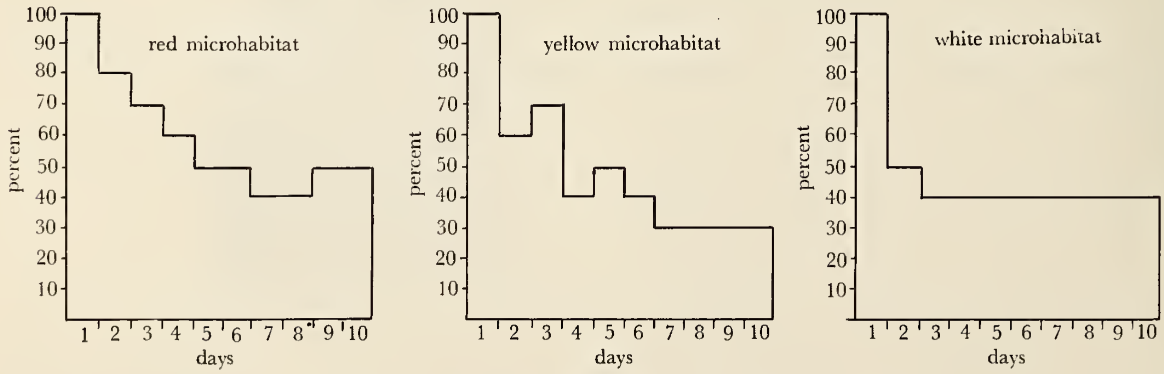

Figure 4

Observations of 30 marked limpets that returned to or remained in designated microhabitats, expressed in percent, August 4 to 14, 1971

Table 1

Frequency and percent of all resting *Acmaea digitalis* observed having contact with one or more limpets within the three studied microhabitats, and marked *Acmaea digitalis* observed in contact with other limpets outside the three studied microhabitats. Observations also include those *Acmaea digitalis* resting without contact both inside and outside of the studied microhabitats. N = 573

Date	number of limpets in contact within 3 studied microhabitats	number of limpets not in contact within 3 studied microhabitats	number of marked limpets in contact outside of 3 studied microhabitats	number of marked limpets not in contact outside of 3 studied microhabitats
August 4	30	4	–	–
August 5	34	5	–	–
August 6	38	2	12	1
August 7	34	6	11	5
August 8	37	4	11	5
August 9	32	7	13	4
August 10	34	6	14	4
August 11	30	9	13	4
August 12	36	3	12	4
August 13	34	7	10	4
August 14	27	11	10	6
Mean	33.3	5.8	11.7	4.1
Percent	85.1	14.9	74.2	25.8

reveals that in the white microhabitat a significant percentage of animals oriented with their anterior ends in the 270° - 360° quadrant. This may be attributed to the fact that the particular microhabitat had a wide, flat angle in its lower right hand quarter. Limpets which were foraging below the cluster found easy access in returning, as opposed to the steeper slope above and to the left hand margins of the cluster site. Their movements apparently ended within the group when contact was made with the shell of a resting limpet.

One observation during a receding high tide noted that one limpet while joining the cluster made contact with 2 *Acmaea digitalis* and one *A. scabra,* resting at the edge of the cluster. When these 3 resting limpets were stimulated by the movements of the incoming one, they rotated and shifted their positions slightly to allow it room to position itself.

An obvious phenomenon of this species is its contact behavior; however, as previously indicated, no prior studies have been found. All of the cluster constituents as well as the marked members outside the clusters were observed for contact. Table 1 reports 573 observations of contact with members of the same species. Approximately 85% of those limpets studied within the microhabitat were in contact with one or more other limpets, while approximately 74% were in contact with other limpets outside the 3 specified microhabitats. Again, it is believed that rock topography somewhat influences contact.

Table 2

Orientation frequencies (expressed in percent) of limpets found in quadrants within three studied microhabitats. Orientation position is determined by the degrees to which the limpet's anterior end is pointing

	Yellow Microhabitat					Red Microhabitat					White Microhabitat				
Date	0- 90°	90-180°	180-270°	270-360°	Resting on horizontal plane	0- 90°	90-180°	180-270°	270-360°	Resting on horizontal plane	0- 90°	90-180°	180-270°	270-360°	Resting on horizontal plane [1]
August 4	0	3	4	4	2	1	0	1	2	6	5	1	2	3	–
August 5	3	3	1	0	1	1	3	3	1	6	0	0	6	2	–
August 6	0	4	2	0	3	1	3	6	2	5	4	0	1	4	–
August 7	0	4	4	0	4	2	2	5	1	6	2	2	4	4	–
August 8	2	3	2	3	3	3	4	3	0	7	3	1	4	4	–
August 9	0	3	3	1	3	2	5	3	1	4	3	1	4	4	–
August 10	2	3	0	0	4	0	3	5	3	6	2	4	4	2	–
August 11	0	4	1	1	3	2	3	8	0	5	3	2	3	5	–
August 12	1	3	1	1	4	0	5	4	1	6	0	1	4	7	–
August 13	1	3	0	0	4	2	5	5	1	7	1	2	3	6	–
August 14	1	2	2	0	5	0	4	5	0	6	0	5	3	4	–
Total	10	35	20	10	36	14	37	48	12	64	23	19	38	45	–
Percent	9	31.8	18.4	9	32.6	8	21.2	27.4	6.8	36.5	18.4	15.2	30.4	36	–

°s refer to a vertical plane

[1] no horizontal plane existed in this microhabitat

The latter mentioned percent occurred with marked members outside of the designated cluster sites. Many of these limpets rested in the upper highly fractured areas of the studied habitat providing solitary or at best few suitable resting sites for multiple contacts. Limpets within the cluster sites occurring along the smooth rock surface clearly demonstrated the highest contact phenomenon. In analyzing detailed field sketches of limpet orientation with reference to contact, no one specific part of an animal or its shell appeared to be predominantly in contact with the shells or bodies of other limpets. Mantle as well as shell contact apparently can be made in any orientation position.

In order to further explore this tactile phenomenon, dummy clusters were placed in previously occupied cluster sites. There were no instances where limpets made contact with either of the 2 pseudoclusters. Three limpets did rest within 7 cm of the dummy cluster, but at no time did they make contact.

The last aspect of behavior I considered was that of periodicity. It has been generally assumed that limpets forage daily when covered by the high tide and rest during the low tidal periods. Figure 5 shows the activity periods of *Acmaea digitalis* for a 10 day period. In all 3 clusters the limpets' total days of rest exceeded their total days of movement. The mean resting time for all members studied was 6.3 days, while the mean movement time was 3½ days. The maximum time at rest for any one individual was 9 days, and the longest time of activity during periods of high tide for one individual was 7 days.

Figure 3 demonstrates in consecutive days that in most instances the resting period extends beyond one day. There is also evidence that once the activity period is initiated, it continues uninterrupted during the high tides for an unpredictable length of time. Although there is a general cyclic pattern of rest and movement existing in the population, no one individual showed any synchronized behavior with its neighbors.

A hypothesis that there was no significant difference between the means of the 2 small samples was temporarily assumed. A "t test" of significance was applied to the data summarized in Figure 5 concerning members of the

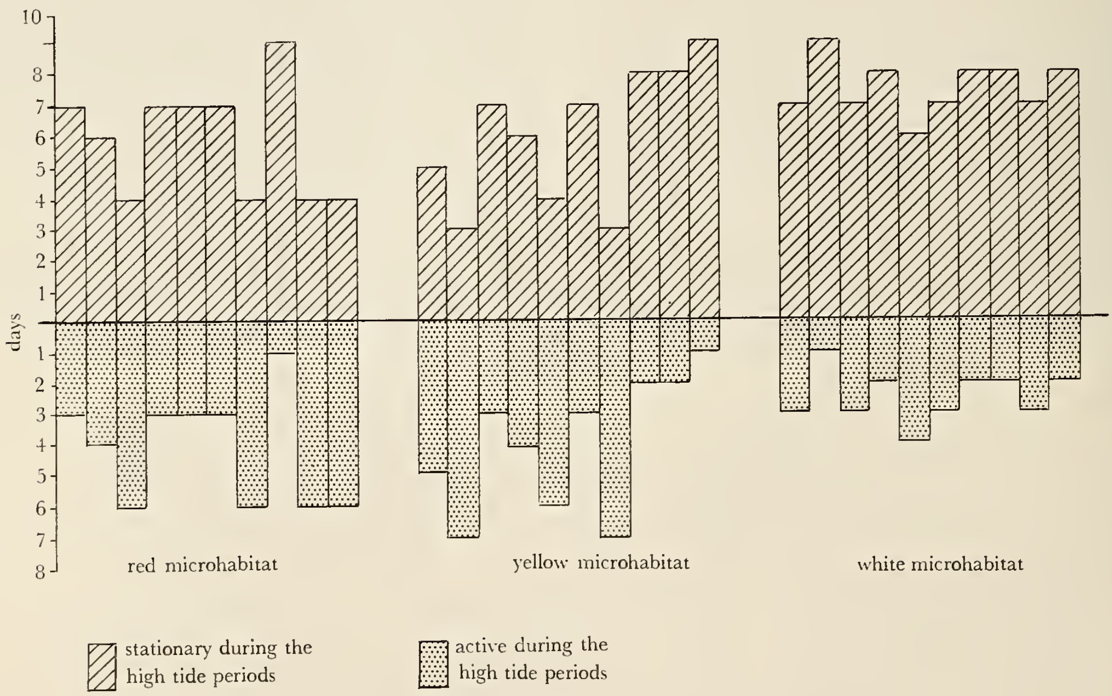

Figure 5

A 10-day study of the movement and resting behavior of 30 marked individuals of *Acmaea digitalis* within 3 studied microhabitats